

Theropod dinosaurs from Argentina

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Abstract. Theropoda includes all the dinosaurs more closely related to birds than to sauropodomorphs (long-necked dinosaurs) and ornithischians (bird-hipped dinosaurs). The oldest members of the group are early Late Triassic in age, and non-avian theropods flourished during the rest of the Mesozoic until they vanished in the Cretaceous-Palaeogene mass extinction. Theropods radiated into two main lineages, Ceratosauria and Tetanurae, which are well represented in Cretaceous rocks from Argentina. Ceratosaurians are the most taxonomically diverse South American non-avian theropods, including small to large-sized species, such as the iconic horned dinosaur *Carnotaurus*. Argentinean tetanurans are represented by multiple lineages that include some of the largest carnivorous dinosaurs known worldwide (carcharodontosaurids), the enigmatic large-clawed megaraptorans, and small to medium-sized species very closely related to avialans (e.g. unenlagiids). The Argentinean non-avian theropod record has been and is crucial to understand the evolutionary and palaeobiogeographical history of the group in the southern continents during the Mesozoic.

Key words. Dinosauria, Saurischia, phylogeny, evolution, palaeobiogeography.

Resumen. Theropoda incluye a todos los dinosaurios más cercanamente relacionados a las aves que a los sauropodomorfos (dinosaurios de cuello largo) y ornithisquios (dinosaurios con cadera de ave). Los miembros más antiguos del grupo son del Triásico Tardío temprano, y los terópodos no-avianos florecieron durante el resto del Mesozoico hasta su desaparición en la extinción masiva del Cretácico-Paleógeno. Los terópodos radiaron en dos linajes principales, Ceratosauria y Tetanurae, los cuales están bien representados en las rocas cretácicas de Argentina. Los ceratosaurios son los terópodos no-avianos taxonómicamente más diversos de América del Sur, incluyendo especies de pequeño a gran tamaño, tales como el icónico dinosaurio con cuernos *Carnotaurus*. Los tetanuros argentinos están representados por múltiples linajes que incluyen a algunos de los dinosaurios carnívoros más grandes conocidos a nivel mundial (carcharodontosáuridos), los enigmáticos megaraptores y especies de pequeño a mediano tamaño muy cercanamente relacionadas a las aves (e.g. unenlagiidos). El registro de terópodos no-avianos argentinos ha sido y es crucial para entender la historia evolutiva y paleobiogeográfica del grupo en los continentes del sur durante el Mesozoico.

Palabras clave. Dinosauria, Saurischia, filogenia, evolución, paleobiogeografía

INTRODUCTION

Theropoda is the clade that includes all the dinosaurs more closely related to birds than to sauropodomorphs (long-necked dinosaurs) and ornithischians (bird-hipped dinosaurs). Most theropods were carnivorous forms, but some were secondarily herbivorous (e.g. *Chilesaurus*, ornithomimosaurs, therizinosaurs). Theropods appear for the first time in the early Late Triassic (ca. 231 Ma) and flourished during the rest of the Mesozoic. The vast majority of the theropod lineages were vanished away by the Cretaceous–Palaeogene mass extinction event (ca. 66 Ma) and only one clade survives nowadays with approximately 10,000 species, the birds. The evolutionary history of non-avian dinosaurs has been mainly known from the Northern Hemisphere record until the 1960's and mainly the 1980's, when the explorations of José F. Bonaparte and subsequently by several Argentinean palaeontologists

resulted in the discovery of an abundant and diverse Jurassic and Cretaceous theropod assemblage, mainly in Patagonian provinces (Novas *et al.*, 2013). Before the exponential sequence of discoveries that started in the late XX century, the theropod record from Argentina was based on the enigmatic *Genyodectes serus* from the Early Cretaceous of Chubut, which was the first theropod to be described for the country (Woodward, 1901). As a result, beyond some sporadic reports of fragmentary bony specimens (e.g. *Unquillosaurus ceibalii*) and ichnites (e.g. *Sarmientichnus scagliai*), the theropod faunas of Argentina remained almost unknown during most of the last century. The discoveries that started during the 1980's show that the Cretaceous theropod assemblages of South America resembled those from other regions of Gondwana (e.g. India, Africa), but contrast with those from North America and Asia (Bonaparte & Novas, 1985; Bonaparte & Kielan-Jawarowska, 1987). The non-avian theropod record of Argentina spans from the Carnian up to the Maastrichtian, thus documenting the complete 165 Ma of evolutionary history of the group. Here we provide a brief update of our current understanding of the higher-level phylogenetic relationships of theropods, and then a summary of the Argentinean record of the group.

Institutional abbreviations. MACN-Pv, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Paleontología de Vertebrados, Buenos Aires, Argentina.

PHYLOGENETIC INTERRELATIONSHIPS OF NON-AVIAN THEROPODS

The phylogenetic relationships of the non-avian theropod dinosaurs have been explored by multiple, independent cladistic analyses in the last 30 years. The vast majority of these analyses have agreed in the recognition of several theropod clades, such as Coelophysoidea, Abelisauroida (Abelisauridae + Noasauridae), Spinosauroida (megalosaurs + spinosaurs), Allosauroida (allosaurs + carcharodontosaurids) and Coelurosauria, a highly diverse group that includes Megaraptora (but see below), Tyrannosauroida, Compsognathidae, Ornithomimosauria, Alvarezsauroida, Therizinosauroida, Oviraptorosauria, Scansoriopterygidae, Dromaeosauridae, Troodontidae, and Aves (e.g. Carrano *et al.*, 2012; Pol & Rauhut, 2012; Nesbitt & Ezcurra, 2015; Novas *et al.*, 2015; Xu *et al.*, 2015; Brusatte & Carr, 2016) (Fig. 1). However, the interrelationships among all these clades and in some cases their taxonomic content has been matter of considerable debate.

Coelophysoidea represents the most basal branch of Neotheropoda (Fig. 1). Current phylogenetic studies found strong evidence favouring the placement of ceratosaurians (*Ceratosaurus* and abelisauroids) closer to tetanurans than to coelophysoids, resulting in a monophyletic Averostra (i.e. Ceratosauria + Tetanurae, excluding Coelophysoidea) (Paul, 2002; Rauhut, 2003; Ezcurra, 2006). Within Tetanurae, most analyses recovered Allosauroida more closely related to Coelurosauria than to Megalosauroida (e.g. Carrano *et al.*, 2012). Nevertheless, a recent analysis recovered a monophyletic Carnosauria, being composed of Megalosauroida and Allosauroida to the exclusion of other theropods (Rauhut *et al.*, 2012). The phylogenetic position of the Argentinean theropod *Megaraptor namunhuaiquii* and its kin (e.g. *Aerosteon riocoloradensis*, *Orkoraptor burkei*) has been a contentious issue since the discovery of this taxon (Novas, 1998; Benson *et al.*, 2010; Novas *et al.*, 2013, 2015). The recognition of a monophyletic Megaraptora (Benson *et al.*, 2010) has not helped to reach a consensus about the phylogenetic position of the group and in recent analyses they have been alternatively found as deeply nested within Allosauroida (Benson *et al.*, 2010; Carrano *et al.*, 2012) or Tyrannosauroida (Novas *et al.*, 2013; Porfiri *et al.*, 2014), or as the most basal coelurosaurs (Novas *et al.*, 2015) (Fig. 1).

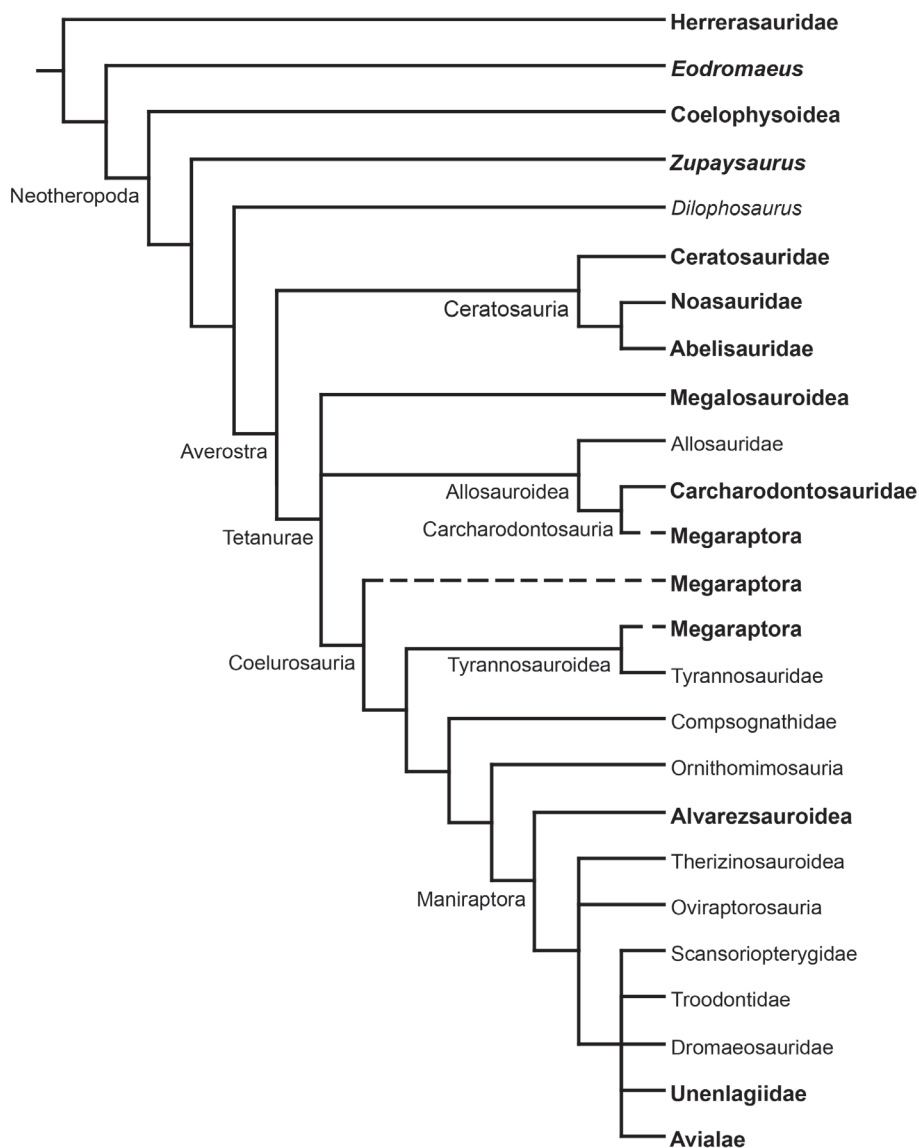


Figure 1. Phylogenetic relationships of theropod dinosaurs based on the phylogenetic results of Nesbitt & Ezcurra (2015), Carrano *et al.* (2012), and Choiniere *et al.* (2013), the alternative positions of megaraptorans (in dashed lines) are based on Benson *et al.* (2010) and Novas *et al.* (2013, 2015), and the unresolved relationships of derived maniraptorans follow the results of Hu *et al.* (2009), Agnolín & Novas (2011), Xu *et al.* (2011, 2015), and Godefroit *et al.* (2013) (see text).

Tyrannosauroids (Proceratosauridae + Tyrannosauridae) are generally found as the most basal members of Coelurosauria, being the sister-taxon of Compsognathidae and a clade composed of Ornithomimosauria and more derived forms (e.g. Choiniere *et al.* 2013). Among these more derived forms, Oviraptorosauria, Therizinosauroidae and Alvarezsauridae are frequently recovered as the successive sister-taxa of Avialae and its more closely related clades (e.g. Xu *et al.*, 2015). The position of the closest clade to Avialae has been also matter of considerable debate in recent years.

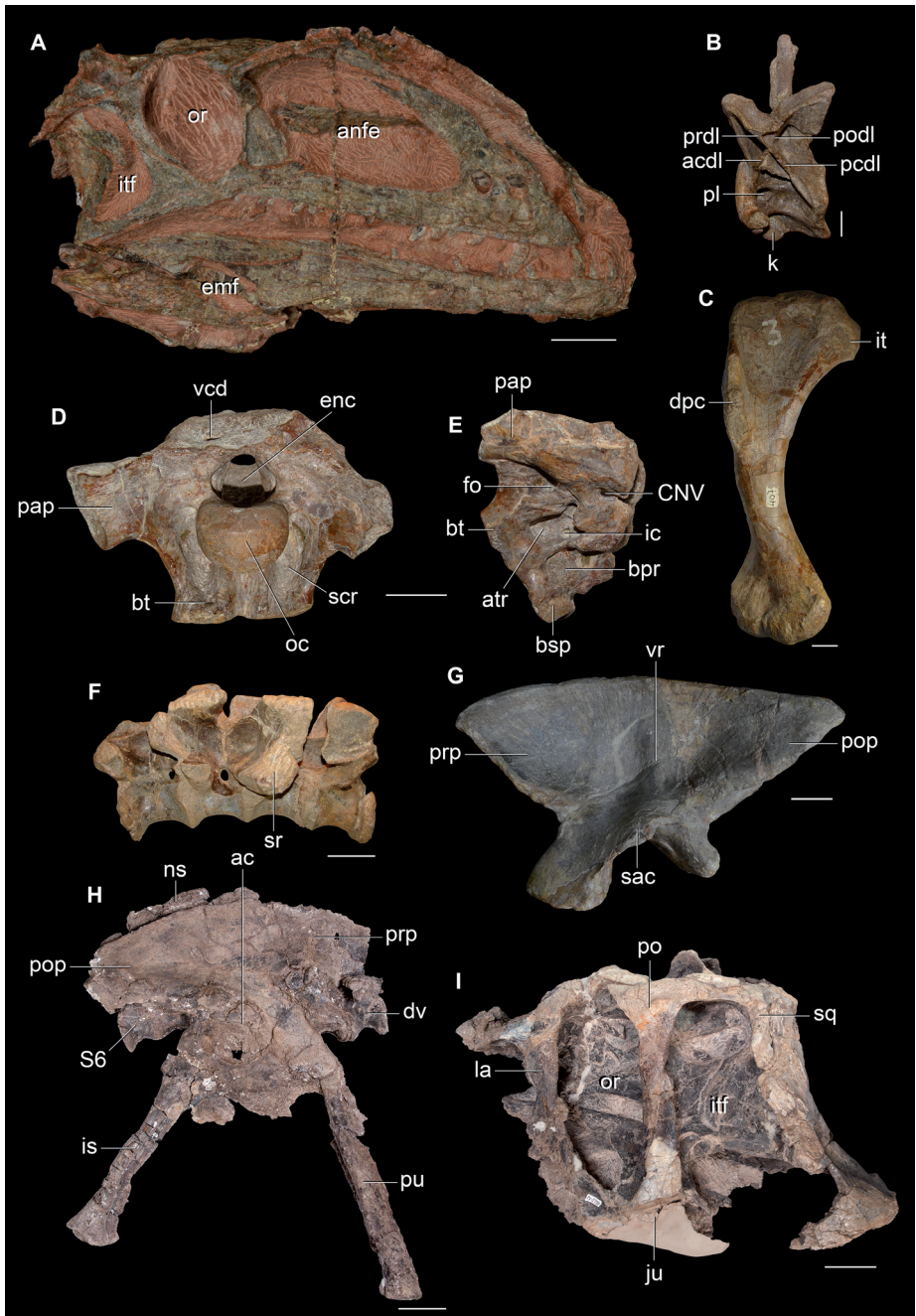
A monophyletic Deinonychosauria (Dromaeosauridae + Troodontidae) has been repeatedly found as the sister-taxon of *Archaeopteryx lithographica* and its kin during the 1990's and 2000's (e.g. Gauthier, 1986; Makovicky *et al.*, 2005). However, Hu *et al.* (2009) recovered the tiny and presumably arboreal scansoriopterygids as the non-avian theropods most closely related to avialans. Subsequently, Agnolín and Novas (2011, 2013) found scansoriopterygids more closely related to oviraptorosaurs than to other theropods and unenlagiids as the sister-taxa of avialans. The latter hypothesis contrasts with previous results (e.g. Makovicky *et al.*, 2005) but agreed with the early proposal of Novas & Puerta (1997) about the close affinities between *Unenlagia comahuensis* and birds. Xu *et al.* (2011) recovered *Archaeopteryx lithographica* and its kin as more closely related to dromaeosaurids and troodontids than to birds (i.e. within Deinonychosauria), thus sharply contrasting with the historical view of this species as the most basal bird. By contrast, Xu *et al.* (2011) found scansoriopterygids as the most basal branch of Avialae. More recently, Xu *et al.* (2015) recovered a similar result, in which deinonychosaurs (including *Archaeopteryx lithographica*) were more closely related to avialans than to other coelurosaurs, but this time to the exclusion of scansoriopterygids. Finally, Godefroit *et al.* (2013) found troodontids as more closely related to avialans than to dromaeosaurids.

In conclusion, there is a general consensus in the monophyly of most of the main theropod lineages and the higher-level phylogenetic relationships (i.e. the monophyly of Averostra, Coelurosauria, Maniraptora). However, the placement of Megaraptora and the most immediate sister-taxa to Avialae are still strongly contentious topics (Fig. 1) and will probably attract a considerable amount of research in future years.

TRIASSIC THEROPODS

The oldest known dinosaur-bearing beds are recorded in the upper Carnian Ischigualasto Formation of NW Argentina (San Juan and La Rioja provinces) and approximately coeval units of Brazil, India and Zimbabwe. The Ischigualasto dinosaur assemblage includes representatives of Theropoda, namely *Eodromaeus murphi* and probably *Herrerasaurus ischigualastensis*. *Eodromaeus murphi* is a small species originally described as a non-neotheropod theropod (Martínez *et al.*, 2011) and subsequent analyses bolstered this result (e.g. Nesbitt & Ezcurra, 2015). The phylogenetic position of *Herrerasaurus ischigualastensis* (body length ca. 6 m) and its kin is variable in different analyses, being alternatively recovered as either the most basal saurischians or theropods. In any case, herrerasaurids show cranial

Figure 2 (Next page). The Triassic and Jurassic theropods *Zupaysaurus rougieri* (A), *Condorraptor currumili* (B), *Piatnitzkysaurus floresi* (C–G), and *Euabelisaurus mafi* (H, I). Skull in right lateral view (A), posterior cervical in left lateral view (B), right humerus in anterior view (C), braincase in posterior (D) and right lateral (E) views, sacrum in left lateral view (F), left ilium in lateral view (G), and pelvic girdle and skull in right lateral (H) and left lateral (I) views. Abbreviations: ac, acetabulum; acdl, anterior centrodiapophyseal lamina; anfe, antorbital fenestra; atr, anterior tympanic recess; bpr, basipterygoid recess; bsp, basipterygoid process; bt, basal tuber; CNV, passage of cranial nerve V; dpc, deltopectoral crest; dv, dorsal vertebra; emf, external mandibular fenestra; enc, endocranial cavity; fo, fenestra ovalis; ic, entrance of the internal carotid artery; is, ischium; it, internal tuberosity; itf, infratemporal fenestra; ju, jugal; k, keel; la, lacrimal; ns, neural spine; oc, occipital condyle; or, orbit; pap, paroccipital process; pcdl, posterior centrodiapophyseal lamina; pl, pleurocoel; po, postorbital; podl, postzygodiapophyseal lamina; pop, postacetabular process; prdl, prezygodiapophyseal lamina; prp, preacetabular process; pu, pubis; S6, sixth sacral vertebra; sac, supraacetabular crest; scr, subcondylar recess; sq, squamosal; sr, sacral rib; vcd, entrance of the vena capitis dorsalis; vr, vertical ridge. Scale bars equal 5 cm in (A, F, G, I), 2 cm in (B, C, D, E), and 10 cm in (H). Photographs (H, I) courtesy of D. Pol.



character-states probably related to predatory habits that resemble the condition in later tetanuran theropods (Sereno & Novas, 1993). *Eoraptor lunensis*, from the same geological unit, has been historically considered a theropod, but recent analyses have found it as a basal sauropodomorph (Martínez *et al.*, 2011).

The lower–middle Norian Los Colorados Formation (La Rioja Province) overlies the Ischigulasto Formation and four theropod specimens have been recovered from this unit. The most complete of them is the holotype and only known specimen of *Zupaysaurus rougieri*, which is represented by a fairly complete skull with a partial postcranium (Fig. 2A). *Zupaysaurus rougieri* is a medium-sized animal (skull length ca. 45 cm) that was originally interpreted as a basal tetanuran (Arcucci & Coria, 2003), but subsequently found as one of the most basal successive sister taxa of *Averostra* (Nesbitt & Ezcurra, 2015). Other two specimens from the same unit belong to indeterminate theropods, represented by a partial postcranium (Bonaparte, 1972) and a fragmentary femur (Novas, 1993), respectively. The fourth specimen is a tiny theropod (astragalar width 7 mm) currently under description, which is represented by partial hindlimbs and nested within Coelophysidae (MDE unpublished data). In addition, Martínez *et al.* (2015) preliminary reported the remains of an unnamed coelophysoid from the upper Norian Quebrada del Barro Formation of the Marayes-El Carrizal Basin in San Juan Province.

JURASSIC THEROPODS

The Jurassic theropod record of Argentina is restricted to the Lower-Middle Jurassic Cañadón Asfalto and Upper Jurassic Cañadón Calcáreo formations of the Chubut Province. Three named species and an unnamed form currently compose the theropod assemblage of the former unit, namely the ceratosaur *Eoabelisaurus mefi* (Pol & Rauhut, 2012) (Fig. 2H, I), the basal tetanurans *Piatnitzkysaurus floresii* (Fig. 2C–G) and *Condorraptor currumili* (Fig. 2B) (Bonaparte, 1986; Rauhut, 2005), and a still preliminary reported, unnamed basal tetanuran (Rauhut & Pol, 2011). *Eoabelisaurus mefi* is a medium-sized theropod (total length 6–6.5 m) originally interpreted as the most basal member of the Abelisauridae, thus predating the oldest record of the clade by more than 40 Ma (Pol & Rauhut, 2012). By contrast, *Eoabelisaurus mefi* has been recovered more recently as the sister-taxon of Abelisauroidae (i.e. Noasauridae + Abelisauridae) by Tortosa *et al.* (2014). The other two named species from the Cañadón Asfalto Formation are similar in size to *Eoabelisaurus mefi* and have been found more closely related to each other than to other theropods, within the family Piatnitzkysauridae (Smith *et al.*, 2007; Carrano *et al.*, 2012). This family have been alternatively recovered at the base of Tetanurae (Smith *et al.*, 2007) or at the base of Megalosauroidae (Carrano *et al.*, 2012). The preliminary reported theropod from the Cañadón Asfalto Formation is a large-sized basal tetanuran represented by a rather complete skeleton that awaits for its formal description (Rauhut & Pol, 2011). In addition, a partial skull of a basal tetanuran different from *Piatnitzkysaurus floresii*, an isolated dentary of a possible ceratosaur, and several theropod teeth have been reported from this unit (Rauhut, 2007; Ezcurra & Pol, 2009).

The bizarre basal tetanuran *Chilesaurus diegosuarezi* was recently described from the uppermost Jurassic of southern Chile (Novas *et al.*, 2015). This species is one of the best known Late Jurassic dinosaurs from the Southern Hemisphere and its unique combination of features suggests the presence of an endemic clade of secondarily herbivorous theropods in south-western Gondwana by the end of the Jurassic. The latest Middle–Late Jurassic theropod record of Argentina is represented by the functionally monodactyl ichinities of *Sarmientichnus scagliai* from the La Matilde Formation of the Santa Cruz Province (Casamiquela, 1964) and a preliminary reported basal tetanuran from the Cañadón Calcáreo Formation of the Chubut Province (Rauhut & Pol, 2011).

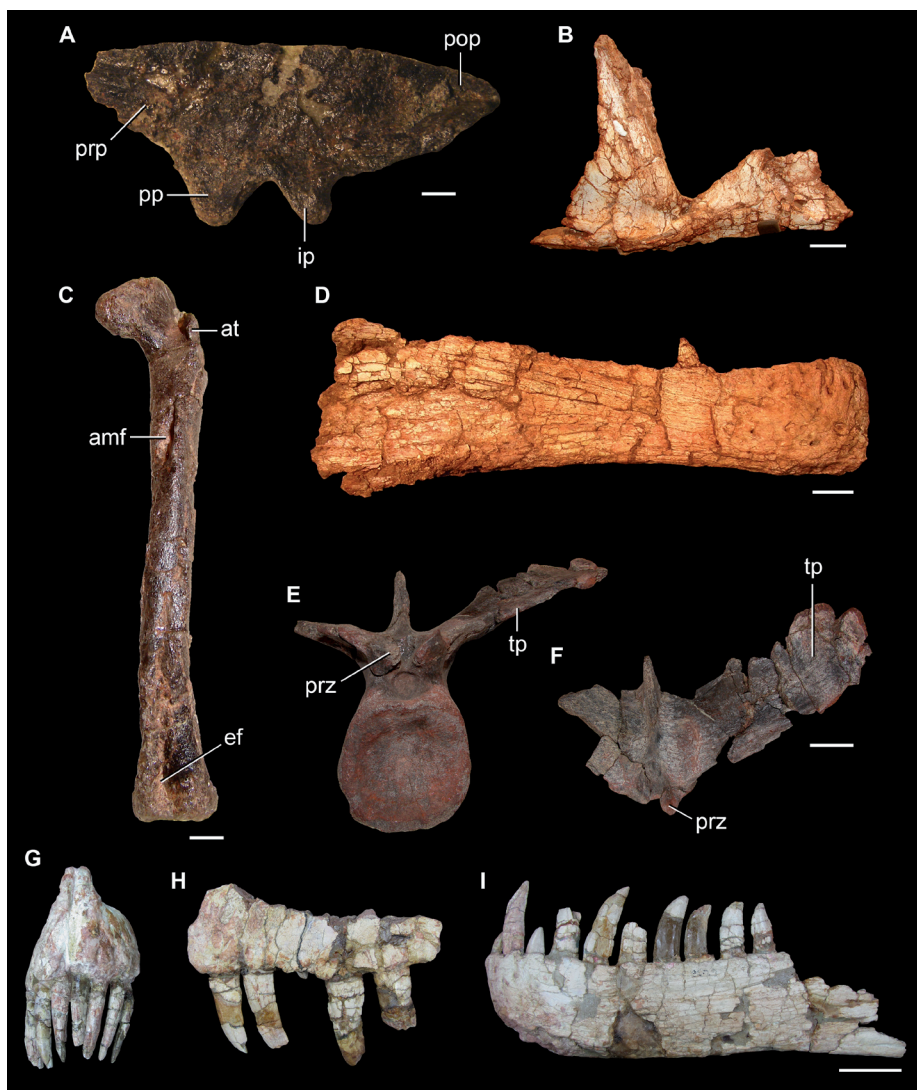


Figure 3. The Early Cretaceous theropods *Ligabueino andesi* (A, C), *Tyrannotitan chubutensis* (B, D), an indeterminate abelisaur (E, F), and *Genyodectes serus* (G–I). Right ilium in medial view (A), right jugal in lateral view (B), left femur in anterior view (C), right dentary in lateral view (D), anterior caudal vertebra in anterior (E) and dorsal (F) views, premaxillae in anterior view (G), and left maxilla (H) and dentary (I) in lateral views. Abbreviations: amf, anteromedial fossa; at, anterior trochanter; ef, extensor fossa; ip, ischiadic peduncle; pp, pubic peduncle; pop, postacetabular process; prp, preacetabular process; prz, prezygapophysis; tp, transverse process. Scale bars equal 2 cm in (A, C), 5 cm in (B, D, G–I), and 2 cm in (E, F).

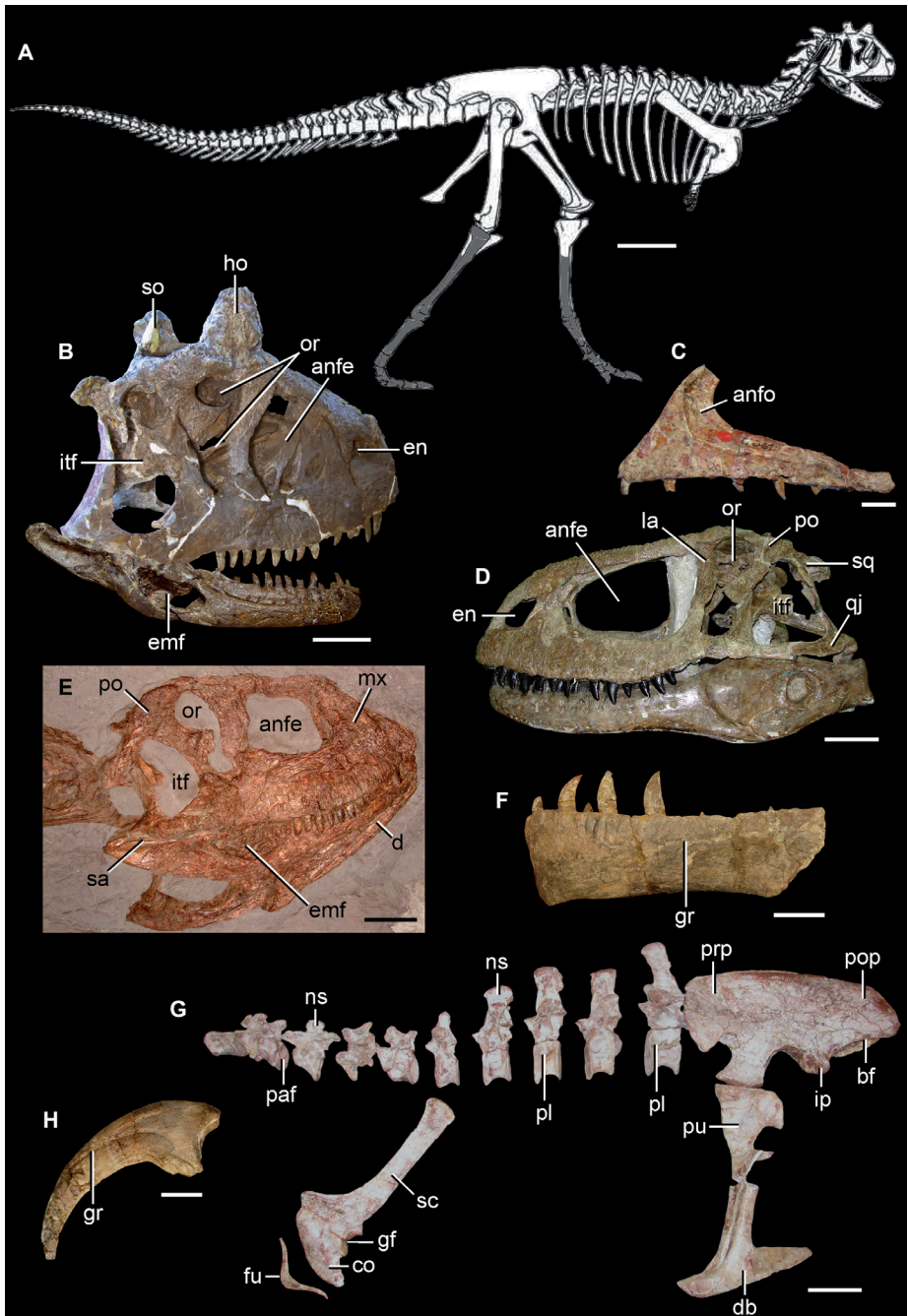
EARLY CRETACEOUS THEROPODS

The Early Cretaceous theropod record from Argentina is restricted to occurrences from Chubut and Neuquén provinces. The oldest Cretaceous theropod-bearing beds of Argentina correspond to those of the Berriasian–Valanginian Bajada Colorada and the upper Valanginian Mulichinco formations (Neuquén Province), which have

yielded scarce remains of preliminary reported basal tetanurans (Apesteguí & Bonaparte, 2004; Gianechini *et al.*, 2011) and an animal with abelisaur affinities (Coria *et al.*, 2010). Although fragmentary, these theropod remains are particularly important because terrestrial Berriasian–Valanginian tetrapods are very poorly sampled worldwide (Ezcurra & Agnolín, 2012). The late Barremian–early Aptian La Amarga Formation possesses some of the best known Early Cretaceous tetrapods from South America, such as the dicraeosaurid sauropod *Amargasaurus cazaui* and the cladotherian mammal *Vincelestes neuquenianus* (Bonaparte, 1996). The theropod record from this unit is currently limited to the tiny partial postcranium of the abelisauroid *Ligabueino andesi* (femoral length 62.4 mm) (Fig. 3A, C) and several isolated teeth comparable with those of large basal tetanurans (Apesteguí, 2007). *Ligabueino andesi* has been recently found within Noasauridae (Tortosa *et al.*, 2014) and a detailed description of its anatomy is currently under preparation by the senior author. Del Corro (1974) described an isolated tooth crown from the Middle–lowermost Late Cretaceous Castillo Formation of the San Jorge Basin, southern Chubut Province, as the holotype of “*Megalosaurus chubutensis*”. Poblete & Calvo (2004) considered “*Megalosaurus chubutensis*” a *nomen vanum* and assigned it possibly to the Carcharodontosauridae. This taxonomic assignment is soundly based on the large size (preserved apicobasal length 64.5 mm and mesiodistal width 34.3 mm) of the crown and the presence of wrinkles adjacent to the distal margin, but these features are highly homoplastic among theropods and we agree with these authors in considering the affinities of the specimen as tentative. Martinelli *et al.* (2007) described isolated teeth and caudal vertebrae of indeterminate theropods from the Albian Cullín Grande Member of the Lohan Cura Formation, Neuquén Province.

The richest diversity of Argentinean Early Cretaceous theropods comes from the Aptian–Albian Cerro Barcino Formation of the Chubut Province. The first theropod specimen described for these beds was the ceratosaur *Genyodectes serus*, which is based on a partial snout of a single specimen (Woodward, 1901; Rauhut, 2004) (Fig. 3G–I). This species has been recently recovered as the sister-taxon of the Late Jurassic North American ceratosaur *Ceratosaurus* (Pol & Rauhut, 2012). More recently, Rauhut *et al.* (2003) described two anterior caudal vertebrae of an abelisaurian (probably abelisaurid) theropod from the Hauterivian–Barremian La Paloma Member of the same formation (Fig. 3E, F). Novas *et al.* (2005) erected the new genus and species *Tyrannotitan chubutensis* based on two partial skeletons from the Aptian Cerro Castaño Member of this formation (Fig. 3B, D). The skeletons that compose the hypodigm of *Tyrannotitan chubutensis* belonged to animals with a total body length of around 13 metres and are the most complete Early Cretaceous theropod specimens known so far from Argentina.

Figure 4 (Next page). The Late Cretaceous abelisauroids *Carnotaurus sastrei* (A, B), *Noasaurus leali* (C), *Abelisaurus comahuensis* (D) and *Skorpiovenator bustingorryi* (E), the carcharodontosaurid *Giganotosaurus carolinii* (F), and the megaraptorans *Aerosteon riocoloradensis* (G) and *Megaraptor namunhuaiquii* (H). Reconstruction of the skeleton (preserved bones in white) in right lateral view (A), skulls in right lateral (B, E) and left lateral (D) views; left maxilla in lateral view (C), left dentary in lateral view (F), partial pre-caudal postcranium in left lateral view (G), and manual ungual I-1 in lateral view (H). Abbreviations: anfe, antorbital fenestra; anfo, antorbital fossa; bf, brevis fossa; co, coracoid; d, dentary; db, distal boot; emf, external mandibular fenestra; en, external naris; fu, furcula; gf, glenoid fossa; gr, groove; ho, horn; ip, ischial peduncle; itf, infratemporal fenestra; la, lacrimal; mx, maxilla; ns, neural spine; or, orbit; paf, posterior articular facet; pl, pleurocoel; po, postorbital; pop, postacetabular process; prp, preacetabular process; pu, pubis; qj, quadratojugal; sa, surangular; sc, scapula; so, supraoccipital eminence; sq, squamosal. Scale bars equal 50 cm in (A), 10 cm in (B, E, F), 1 cm in (C), 5 cm in (H), and 20 cm in (D, G).



LATE CRETACEOUS THEROPODS

The Late Cretaceous theropod record from Argentina is considerably richer than those from older Mesozoic outcrops of the country and represents the richest theropod sample from Gondwana in terms of quantity and quality of specimens (Novas *et al.*,

2013). The most comprehensive knowledge of an early Late Cretaceous theropod assemblage comes from the Cenomanian Candeleros Formation of the Neuquén Basin (Neuquén Province). This unit yielded the remains of abelisaurids (*Ekrixinatosaurus novasi*), carcharodontosaurids (*Giganotosaurus carolinii*) (Fig. 4F), basal coelurosaurs (*Bicentenaria argentina*) (Fig. 5A–C), alvarezsaurids (*Alnashetri cerropolicienensis*) and unenlagiids (*Buitreraptor gonzalezorum*) (Fig. 5I, J) (Coria & Salgado, 1995; Calvo *et al.*, 2004; Makovicky *et al.*, 2005, 2012; Novas *et al.*, 2012). Thus, the Candeleros Formation includes the oldest records of alvarezsaurids, unenlagiids, and probably carcharodontosaurids (depending on the affinities of “*Megalosaurus chubutensis*”) for Argentina. The upper Cenomanian–lower Turonian Huincul Formation directly overlies the Candeleros Formation and preserves a theropod assemblage composed of abelisaurids (*Ilokelesia aguadagrandensis*, *Skorpiovenator bustingorryi*: Fig. 4E) and carcharodontosaurids (*Mapusaurus roseae*) (Coria & Salgado, 2000; Coria & Currie, 2006; Canale *et al.*, 2009).

Cenomanian abelisaurids (*Xenotarsosaurus bonapartei*), probable carcharodontosaurids (based on isolated teeth), megaraptorans (a preliminary reported form), basal coelurosaurs (e.g. *Aniksosaurus darwini*: Fig. 5E, G, H) and putative dromaeosaurids (based on isolated teeth) have been also described for the lower member of the Bajo Barreal Formation of the San Jorge Basin (Chubut Province) (Martínez *et al.*, 1986; Martínez & Novas, 2006; Coria & Currie, 2002; Casal *et al.*, 2009). Isolated theropod tooth crowns found in the Cenomanian Bayo Overo Member of the Cerro Barcino Formation represent the hypodigm of “*Megalosaurus inexpectatus*” (del Corro, 1966). These tooth crowns possess a continuously convex mesial margin and a straight distal one, lacking ornamentation on the enamel (MACN-Pv 18172; but two of the original set of four teeth are currently lost). This combination of features suggests that this species could be an abelisaurid and based on the absence of a unique combination of character-states among abelisaurids, “*Megalosaurus inexpectatus*” is here considered a *nomen vanum*.

The Mata Amarilla Formation of the Austral Basin (Santa Cruz Province) has been interpreted as upper Campanian–lower Maastrichtian in age on the basis of its micropalaeontological content, but an older age (Cenomanian) was subsequently proposed on the basis of its dinosaurian and dipnoan content (Novas *et al.*, 2002) and a recent radioisotopic dating yielded a middle Cenomanian age for this unit (Varela *et al.*, 2012). The theropod assemblage of the Mata Amarilla Formation (referred to as Pari Aike Formation in some previous contributions) is composed of an abelisauroid (*Austrocheirus isasii*) and a megaraptoran (*Orkoraptor burkei*) (Novas *et al.*, 2008; Ezcurra *et al.*, 2010).

The middle Turonian Cerro Lisandro Formation directly overlies the Huincul Formation and has a theropod record limited to an indeterminate, medium-sized abelisauroid (Coria *et al.*, 2006). Immediately overlying this unit, the Portezuelo Formation is dated as late Turonian–early Coniacian in age and preserves a very good sample of middle Late Cretaceous theropods. The carnivorous dinosaur assemblage of this unit includes abelisauroids (an unnamed form), megaraptorans (*Megaraptor namunhuaiquii*: Fig. 4H), alvarezsaurids (*Patagonykus puertai*), and unenlagiids (*Neuquenraptor argentinus*, *Pamparaptor micros*, *Unenlagia comahuensis*: Fig. 5D, *Unenlagia paynemili*), thus closely resembling the taxonomic richness and composition of the older Candeleros Formation.

The holotype and only known specimen of the megaraptoran *Aerosteon riocoloradensis* (Serenó *et al.*, 2008) (Fig. 4G) and isolated tooth crowns of a cf. Carcharodontosauridae and an indeterminate maniraptoran (Canudo *et al.*, 2009) come from the upper Coniacian–lower Santonian Plottier Formation (Neuquén and Mendoza provinces) of the Neuquén Basin (Novas *et al.*, 2013). This geological

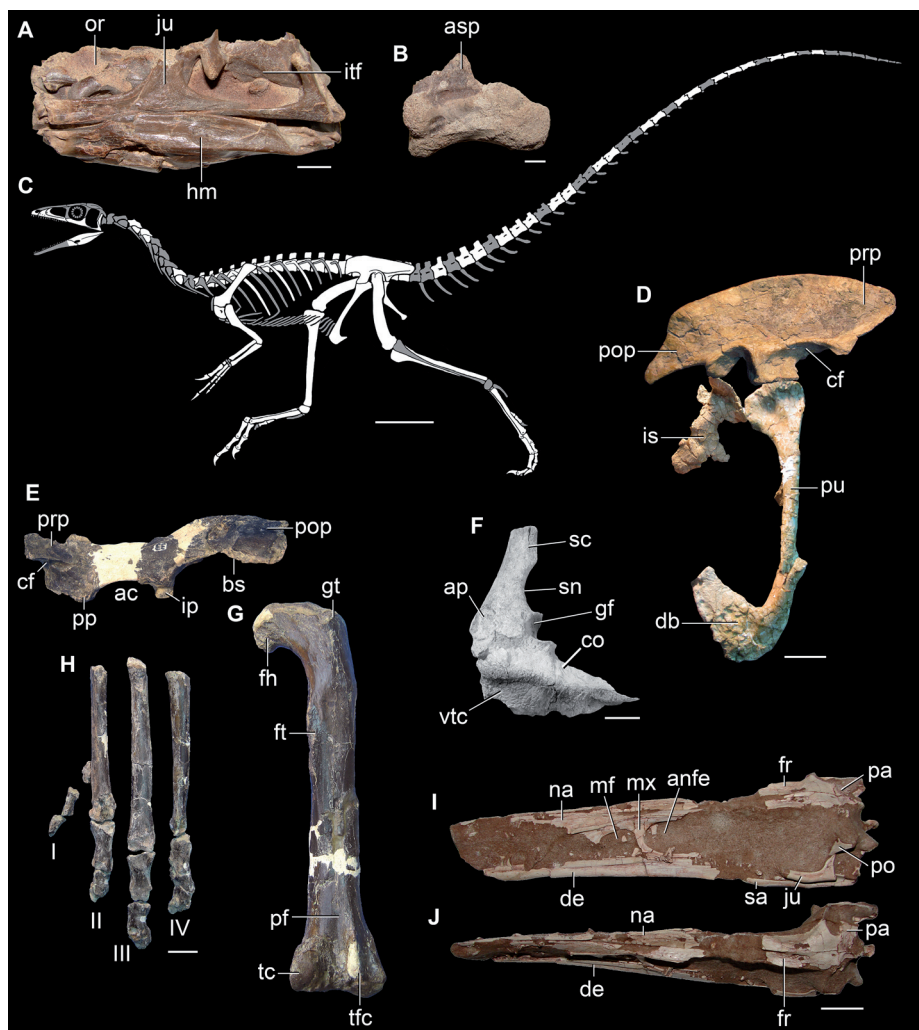


Figure 5. The Late Cretaceous small to medium-sized coelurosaurs *Bicentenaria argentina* (A–C), *Unenlagia comahuensis* (D), *Aniksosaurus darwini* (E, G, H), *Bonapartenkykus ultimus* (F), and *Buitreraptor gonzalezorum* (I, J). Posterior half of the skull in left lateral view (A), right astragalus in anterior view (B), reconstruction of the skeleton (preserved bones in white) in left lateral view (C), right hemipelvis in lateral view (D), left ilium in lateral view (E), left scapula and coracoid in lateral view (F), right femur in posterior view (G), partial right foot in anterior view (H), and skull in left lateral (I) and dorsal (J) views. Abbreviations: I–IV, pedal digits I–IV; ac, acetabulum; anfe, antorbital fenestra; ap, acromial process; asp, ascending process; bs, brevis shelf; cf, cuppedicus fossa; co, coracoid; db, pubic boot; de, dentary; fh, femoral head; fr, frontal; ft, fourth trochanter; gf, glenoid fossa; gt, greater trochanter; hm, hemimandible; ip, ischial peduncle; is, ischium; itf, infratemporal fenestra; ju, jugal; mf, maxillary fenestra; mx, maxilla; na, nasal; or, orbit; pa, parietal; pf, popliteal fossa; po, postorbital; pop, postacetabular process; pp, pubic peduncle; prp, preacetabular process; pu, pubis; sa, surangular; sc, scapula; sn, scapular notch; tc, tibial condyle; tfc, tibiofibular crest; vtc, ventral tilting of coracoid. Scale bars equal 1 cm in (A), 5 mm in (B), 20 cm in (C), 5 cm in (D, F), and 2 cm in (E, G, H–J). Skeletal reconstruction (C) made by Emilio L. Rolandi, and photograph (D) courtesy of F. Brissón Egli.

unit is directly overlaid by the middle–upper Santonian Bajo de la Carpa Formation (Río Negro and Neuquén provinces), which is worldwide known for its diverse non-dinosaurian fauna (Bonaparte, 1991). The non-avian theropod record of the Bajo de la Carpa Formation is composed of noasaurids (*Velocisaurus unicus*), abelisaurids (e.g. *Viavenator exxoni*), a preliminary reported possible carcharodontosaurid, and alvarezsaurids (*Alvarezsaurus calvoi*, *Achillesaurus manazzoni*) (Bonaparte, 1991; Martinelli & Vera, 2007; Porfiri *et al.*, 2008; Fillipi *et al.*, 2016). The early Campanian beds of the Neuquén Basin crop out as the Anacleto Formation (Río Negro and Neuquén provinces), which has a theropod assemblage represented by medium to large-sized abelisaurids (e.g. *Abelisaurus comahuensis*: Fig. 4D, *Aucasaurus garridoi*) (Bonaparte & Novas, 1985; Coria *et al.*, 2002).

The theropod assemblages immediately before the Cretaceous–Palaeogene mass extinction (i.e. Campanian–Maastrichtian) are widely represented in Patagonia and northern Argentina. The Maastrichtian Allen Formation of the Neuquén Basin (Río Negro Province) has a diverse tetrapod fauna that includes abelisaurids (*Quilmesaurus curriei*), alvarezsaurids (e.g. *Bonapartenykus ultimus*: Fig. 5F), and large-sized unenlagiids (*Austroraptor cabazai*) (Coria, 2001; Novas *et al.*, 2009; Agnolín *et al.*, 2012). The Maastrichtian La Colonia Formation of the Chubut Province has yielded the most complete and well preserved theropod known so far from Gondwana, the abelisaurid *Carnotaurus sastrei* (Bonaparte, 1985) (Fig. 4A, B). In northern Argentina, the large maniraptoran *Unquillosaurus ceiballi* comes from the Campanian Los Blanquitos Formation (Powell, 1979) and the small noasaurid *Noasaurus leali* from the Campanian–Maastrichtian Lecho Formation (Fig. 4C), both from Salta Province (Bonaparte & Powell, 1980).

A recently and preliminary reported theropod assemblage from the Upper Cretaceous Los Llanos Formation of the Bermejo Basin (La Rioja Province) includes abelisaurids, maniraptorans, and an indeterminate averostran (Fiorelli *et al.*, 2014). A large partial tooth crown of an indeterminate theropod was described for the Puerto Yeruá Formation (Entre Ríos Province), but the age of the unit is poorly constrained as Cretaceous (de Valais *et al.*, 2003).

MACROEVOLUTIONARY HISTORY OF THE GROUP BASED ON THE GONDWANAN RECORD

The oldest known Argentinean predatory dinosaurs, recovered in the Ischigualasto Formation (e.g. *Eodromaeus*, *Herrerasaurus*), distinctly differ morphologically from the approximately 10–15 million years younger Triassic theropods of the Los Colorados Formation (*Zupaysaurus rougieri*, a still unnamed coelophysoid). This difference implies a replacement in the composition of the carnivorous dinosaur faunas before the Triassic–Jurassic mass extinction, resembling the pattern observed in coeval beds of India (Novas *et al.*, 2011). The vast majority, if not all, of the averostran lineages should have originated during the Early–Middle Jurassic, but the Jurassic theropod record of Gondwana is currently restricted to non-coelurosaurians averostrans (e.g. abelisaurids, piatnitzkysaurids). By contrast, the Jurassic Laurasian record is taxonomically richer and includes basal ceratosaurians, basal tetanurans, and several coelurosaurian clades (e.g., tyrannosauroids, compsognathids, scansoriopterygids, archaeopterygids).

The considerably richer Late Cretaceous Gondwanan non-avian theropod record, when compared with that from the Triassic to Early Cretaceous, allowed Novas *et al.* (2013) to explore the late macroevolutionary history of the clade. These authors found high extinction indices in the Cenomanian–Coniacian time span, but only the index for the Turonian–Coniacian boundary significantly departed from background

extinction levels. In the Cenomanian-Turonian spinosaurids, carcharodontosaurids, and several basal abelisaurid and coelurosaurians lineages went extinct, which is part of a faunal turnover also observed in other vertebrate groups (e.g. dipnoans, rebbachisaurid sauropods, crocodylomorphs, turtles) (Novas *et al.*, 2005). A different taxonomic selectivity between the Cenomanian and Turonian-Coniacian turnovers suggests that they were different processes acting over several million years, rather than a single extinction event. No Cenomanian or Turonian-Coniacian extinctions are evident in the theropod record of the northern continents, but some authors have documented important changes in the terrestrial vertebrate assemblages of Laurasia by Cenomanian times (e.g. Jacobs & Winkler, 1998). By the end of the Late Cretaceous, both Gondwanan and Laurasian theropod assemblages share a similar macroevolutionary pattern, consisting of a continuous increase of extinction levels until reaching the Cretaceous-Palaeogene boundary, and a peak in species origination by the end of the Campanian. Gondwana possesses a Santonian-Maastrichtian dinosaur faunal composition that clearly differs from that previous to the Turonian-Coniacian extinction event, including the presence of abelisaurids and unenlagiids as the top predators of these latest Cretaceous assemblages in Argentina (Coria, 2001; Novas *et al.*, 2009).

THEROPOD PALAEOBIOGEOGRAPHY

The description of abelisaurids during the 1980s and 1990s from Cretaceous beds of South America, India and Madagascar suggested that these theropods were abundant, diverse and widespread in Gondwana (Bonaparte, 1996). This evidence supported the interpretation that Gondwana remained geographically isolated from Laurasia during most of the Cretaceous prior to the Campanian-Maastrichtian (Bonaparte & Kielan-Jawarowska, 1987). However, discoveries of purported Gondwanan lineages (e.g. abelisaurids, spinosaurids, carcharodontosaurids) in Laurasian territories blurred the sharp faunal distinctions once recognized between southern and northern landmasses. Several authors attempted to explain these anomalous occurrences describing the presence of temporary terrestrial land-bridges either between Europe-Africa, North America-South America, and Asia-Australia, thus allowing north-south faunal interchanges at different moments of the Cretaceous. Ezcurra & Agnolín (2012) proposed the Eurogondwanan hypothesis, in which the European region had a close biogeographical affinity with Gondwana during the Berriasian-Hauterivian time-span, allowed by a connection through Africa. After the Hauterivian, several Eurogondwanan tetrapod clades made their appearance in Asiamerica (e.g. megaraptorans, carcharodontosaurids, spinosaurids). This biogeographic pattern was interpreted as evidence for the coalescence of the European region with Asiamerica during the Barremian. These authors proposed that this purported European-Asiamerican faunistic interchange occurred after a short interval of biogeographical isolation of the European region from Gondwana, thus allowing the dispersal of Eurogondwanan taxa into Asiamerica but preventing the immigration of Laurasian taxa into Gondwana.

Ezcurra & Agnolín (2012) found that Europe possessed closer biogeographical affinities with the southern landmasses during the Campanian-Maastrichtian rather than with Asiamerica. The biogeographical re-connection of the European region and South America via Africa during the Campanian-Maastrichtian is supported by the presence of Laurasian tetrapod lineages in the Campanian-Maastrichtian of South America and Antarctica (e.g. hadrosaurid ornithischians). This model constitutes an alternative to the traditional hypothesis of a dispersal event between North America and South America via a terrestrial bridge during the latest Cretaceous (Bonaparte,

1984). Future palaeogeographic research and work on the latest Cretaceous terrestrial faunas of South America may shed light on the provenance of the supposed Laurasian immigrant taxa into the southern continents.

FUTURE DIRECTIONS

The intensive discovery and description of theropod dinosaurs in Argentina is relatively recent in comparison with more than 150 years of continuous research in the Northern Hemisphere. The Late Cretaceous record of theropods, mainly in Patagonia, has considerably increased in the last 20 years and multiple ceratosaurs, allosauroids and coelurosaurs are currently known from these beds. By contrast, the Triassic, Jurassic and Early Cretaceous neotheropod record is still scarce. The discovery of new specimens from this temporal span (e.g. Los Colorados, Laguna Colorada, Cañadón Calcáreo, Bajada Colorada, La Amarga formations), but in parallel with further sampling in Upper Cretaceous beds, seems to be imperative to nourish a more comprehensive understanding of the evolutionary history of Theropoda in the southern continents, including the early evolution of clades such as Carcharodontosauridae, Megaraptora and Unenlagiidae. Such discoveries may become also relevant to shed light on currently contentious phylogenetic issues, including the higher-level relationships of megaraptorans around the allosauroid-coelurosaur dichotomy and the identity of the closest relatives to avialans. In addition, the sampling in poorly prospected regions of the country (e.g. La Rioja, Santa Cruz provinces) will probably add interesting information about more regional patterns that characterized the evolution of the carnivorous dinosaurs in the southern continents. Beyond new discoveries, the revision of already collected specimens using traditional and modern techniques (e.g. CT-scans) is a symptom of a dynamic and healthy line of research that has considerably contributed to increase our knowledge of the South American theropods and should continue in subsequent decades.

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